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BOTANICAL GAZETTE

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THE NODES OF GRASSES.¹

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(WITH PLATES I AND II)

ALTHOUGH the stems and leaves of grasses have received a good share of attention from anatomists, and the bundles of the internodes are perhaps sufficiently well known, the nodes have been largely neglected. The reason for this may be the supposed difficulty of unraveling the tangle of bundles found in the node, or the obstacles which the sclerified tissues offer to the preparation of satisfactory sections. Yet the nodes are probably the most interesting regions of the grass stem, for they lack the comparative uniformity of the internodes. Since the application of the celloidin method to hard tissues the difficulties of cutting the necessary serial sections have been removed, so that we are now in a position to know intimately the structure of these critical regions of the stem.

The object of the present account is to trace the course of the bundles of the grass stem, and to discuss the significance of certain structures which make their appearance at the nodes, in particular the amphivasal bundles and cambium. The investigation has been confined to forty-five genera, but since these represent the eleven largest tribes and there is a considerable degree of uniformity in structure, the account is believed to represent the family fairly from the standpoint chosen.

The salient features may best be brought out by the description of types selected to illustrate certain points. The first to be considered represents a medium condition as regards both taxonomic position and ecological relations.

¹ Contributions from the Phanerogamic Laboratories of Harvard University. No. 3.

Avena barbata.—At a short distance above a node the stem presents a simple structure compared with that of many grasses, showing just two circles of collateral bundles surrounding a central cavity. The inner circle of bundles lies at the periphery of the central cylinder, which in this genus is not clearly marked off from the cortex. The bundles of the outer circle lie between groups of cells, which above the leaf-sheath bear chlorophyll; they are considerably smaller than the bundles of the inner ring, and from comparison with corresponding bundles in other genera must be regarded as cortical bundles. In the upper part of a node these assume an amphivasal structure and immediately anastomose with one another and with bundles of the inner circle. But just at this level the structure of the stem is further complicated by the entrance of bundles of the leaf-trace, the course of which must now be described. The leaf-sheath in this species extends a little more than 360° around the stem, and contains, as do most of the genera examined, bundles of two distinct sizes: larger ones, alternating with others which are less than half as great in diameter. These two kinds of leaf-trace bundles have a different course in the stem. The larger bundles undergo a profound modification as they enter the stem, as may be seen by comparing *figs. 1* and *2*, in which the magnification is the same. As such a bundle enters the stem it rapidly increases in size, owing to increase in the number of xylem elements. Most of the added elements are tracheids with more or less suberized scalariform or reticulate thickenings, but some parenchyma cells are also present. These elements gradually extend around the sides of the phloem until this is surrounded by xylem, except a small area on its outer side, which is generally occupied by sclerotic fibres belonging to the group which is so well marked in the sheath (*fig. 1*). In certain species, e. g., *Lolium perenne*, these fibres disappear, and the phloem is completely surrounded by xylem. These bundles evidently must be placed in the amphivasal class. As *fig. 2* shows, the phloem enlarges very little, but the xylem increases so much that the bundle may be five or six times as broad in the middle of the node as it is in the leaf-sheath. These bundles are by far the most conspicuous objects in a cross-section of the stem at this level. They have a spindle shape which is not due to their oblique course, for they slant

very slightly from the vertical and do not dip deeply into the central cylinder. The xylem consists so largely of tracheids running irregularly and mixed with parenchyma, that the mass has a considerable resemblance to transfusion tissue. Apparently, this region in a bundle forms an important water-storing organ. A further peculiarity of the bundle at this level is the presence of a distinct bundle-sheath or endodermis,² consisting of cells whose walls are reticulately thickened and suberized. As these larger leaf-trace bundles descend through the node, branches from the anastomoses mentioned above extend outward between the leaf-trace bundles, and probably anastomose with these, though the fusion is not so plain as in *A. sativa*. Below this level the bundles gradually resume the ordinary collateral shape, lose their endodermis, and run down in a single circle through the internode as already described. The smaller leaf-trace bundles also undergo some expansion as they penetrate to the boundary of the central cylinder, but throughout their course they may be distinguished from the larger bundles, not only by their size but by their early turning outward into the cortex and running down to the next node as the cortical bundles described above.

Though it is not plain in *A. barbata* that the larger leaf-trace bundles are joined, soon after their entrance into the stem, by other bundles of the node, in *A. sativa* and in many other grasses it may clearly be made out that on each flank of the leaf-trace bundle another strand applies itself, swinging through an angle, so that its phloem first joins on, then its xylem. In some species, e. g., *Arundo Donax*, two or more bundles join on each flank of the leaf-trace bundle.

Certain features of the cortical strands are more clearly seen in *Panicularia americana*. The cortical nature of these strands is unquestioned, for they run quite outside the central cylinder, in a wide area of lacunar parenchyma (*fig. 7*). As they reach the upper part of a node they anastomose with one another so as to form a transverse ring or girdle (*fig. 8*), which, at a slightly lower level, sends branches to the bundles of the central cylinder, forming nearly or quite amphivasal bundles, though some of them very soon resume

² The term endodermis is here used in the general sense employed by VAN TIEGHEM, rather than in the histological sense proposed by other writers.

the collateral structure which is characteristic of all the bundles of an internode. Further down in the node, the bundles of the leaf-trace enter the central cylinder and the smaller of these anastomose with branches of the nodal complex, and then turn outward to run down through the internode as cortical bundles. The larger leaf-trace bundles behave as in *A. sativa*.

In *Leersia oryzoides* it may plainly be seen from a series of sections, that as each of the smaller leaf-trace bundles enters a node, it is joined by two small bundles from the nodal complex, and this reinforced bundle proceeds downward through the sclerified cortex.

Whether the smaller leaf-trace bundles run down through the cortex, or in the outer region of the central cylinder of an internode, cannot in all cases be determined with certainty, for the boundary of the central cylinder is often poorly marked, and the cortex may be a very narrow zone. Or the boundary of the central cylinder may be marked by a narrow sclerenchymatous ring, and the bundles may lie along this, projecting either towards the inside or the outside. But the position of these bundles inside or outside the central cylinder appears to be a matter of indifference, and in either case they pursue a different course from that of the larger bundles. In a general way it may be stated that the smaller bundles of the leaf-trace, after fusing with bundles from the nodal complex, run downward through the next succeeding internode in the cortex or at its inner border, and at the next node below join with the bundles of the central cylinder. Species to which this statement applies are: *Zizania aquatica*, *Leersia oryzoides*, *Avena barbata*, *A. sativa*, *Panicularia americana*, *P. nervata*, *Agropyron caninum*, *Elymus americanus*, *Triticum sativum*.

The course of the leaf-trace bundles in the grasses, as here described, differs in several respects from the course of such bundles in other families, even in so closely related a family as the sedges, recently described by PLOWMAN (11). VAN TIEGHEM'S second class of cortical bundles (6, p. 751) corresponds the most closely, and is thus described: "Le faisceau médian de la feuille, qui en prend trois, entre directement dans le cylindre central, tandis que les deux latéraux descendent dans l'écorce pour n'entrer dans le cylindre

qu'au nœud suivant." See further his remarks on the monocotyledons.

Phalaris arundinacea, like *Avena*, has the bundles of its internode crowded into an annular area surrounding the fistular pith. As these reach the node they anastomose extensively, and at the same time assume the amphivasal condition, which is shown with especial clearness in the variety *variegata*, *figs. 3 and 4*, the latter more highly magnified in order to show the tendency for bundles to form nests of three or more, enclosed by an armor of sclerified fibres. These amphivasal bundles, though abundant in the nodes, are absent from the internodes.

Arundo Donax may be mentioned as typical of species having several circles of bundles surrounding a central cavity. As the leaf-trace bundles enter the stem they swell out, though not to so great an extent as in *Avena*. The xylem completely encloses the phloem, and the usual suberized sheath of cells with reticulately thickened walls becomes visible. Farther down in the node the leaf-trace bundle is joined on each flank by one or more cauline bundles. The bundles of the latter class are provided with a sheath of heavily thickened cells, and some of them appear to pass through the node without anastomosing with other bundles, though this condition is rare in the members of the family which have fewer bundles. In accordance with the greater thickness of the solid part of the stem, the leaf-trace bundles penetrate more deeply into the central cylinder than in such genera as *Avena*, making their general course conform more nearly to the palm type of VON MOHL. The number of circles of bundles in an internode appears to be dependent on the size of stem characteristic of the species, and to have little value in establishing relationships.

Grasses with a solid stem conform even more nearly to VON MOHL's type, for the largest leaf-trace bundles penetrate nearly to the center of the stem, before curving outward and downward toward the periphery of the central cylinder. STRASBURGER (4) has given an excellent account of the course of the bundles in *Zea Mays*. He distinguishes leaf-trace bundles of five different ranks, and finds that the largest of these penetrate most deeply into the stem, while the smallest merely reach the periphery of the central cylinder.

The increase in complexity of the leaf-trace system over the condition found in *Avena*, seems to be associated with the greater size of the leaf-sheath in *Zea*; just as a large stem generally has several circles of bundles, so a heavy leaf has a better developed bundle system. Most of the bundles in an aerial node of *Zea* are collateral, leaving out of consideration the swollen leaf-trace bundles. STRASBURGER (4, p. 348) finds amphivasal bundles at the point of origin of axillary buds and adventitious roots; I have confirmed his observation in the former case. Much larger and more numerous amphivasal strands are however to be found in the nodes of the axillary branches bearing the ear of corn. One of these bundles is represented in *fig. 5*. It is only in the leafy part of the branch that these occur, for in the "cob" the bundles are collateral, with an exceedingly well-developed phloem, doubtless associated with the transfer of elaborated food. The amphivasal bundles of these branches are as usual bundle fusions, and their occurrence in the reproductive axis of a plant showing few elsewhere, seems to be a point of some significance, especially when we consider that *Zea* is probably a highly organized member of the family.

Zizania aquatica merits special attention on account of certain features which may be regarded as primitive, e. g., the six stamens. In an aerial internode a narrow cortex surrounds the hollow central cylinder, and the two are separated by a ring of sclerified cells. Partly imbedded in this ring are a number of small bundles, some of which project into the cortex and on account of their origin must be regarded as cortical bundles. All the bundles are collateral, and those inside the sclerotic ring lie at different depths within the central cylinder. As would be expected from the aquatic habitat of the plant, the xylem is reduced; in fact, in some instances, it is represented only by a cavity, and in all cases it has its vessels very slightly lignified. The phloem does not share in this reduction. As the node is approached the bundles at the periphery of the central cylinder anastomose, at the same time becoming amphivasal, and a number of transverse strands join up some of the inner bundles of the stele with one another. At this level the leaf-trace bundles enter the stem; they are of at least three ranks, and of these the largest penetrate into the central cylinder, enlarging on the way,

owing to increase in the xylem elements, which come to enclose the phloem more or less completely, as already described for *Avena*. A little further down they are joined on the flanks by several bundles from the internode above, each leaf-trace bundle with its tangle of contributing bundles forming a complex bunch of vascular tissue. A suberized endodermis surrounds the leaf-trace bundles in the node. The second rank of bundles of the leaf-trace also enter the central cylinder, where they are joined by other bundles, but soon return to the periphery of the central cylinder, where they give rise to some of the bundles which run through the next internode below on the border line between the sclerotic ring and the cortex. The smallest bundles of the leaf trace go no deeper than the sclerotic ring, and here fuse with other bundles found in this zone. Thus, the course of the bundles of different rank agrees with what STRASBURGER found in *Zea*. In the lowest part of the node, the very numerous bundles of the sclerotic ring anastomose and proceed downward, greatly reduced in numbers, while the bundles inside the central cylinder also become much fewer, owing to completion of the fusion of the large leaf-trace bundles with cauline strands.

The basal region of the stem has a cortex which differs from the aerial parts in being much broader and more spongy, on account of the large intercellular spaces. At any of the basal nodes the central cylinder is bounded by an endodermis, consisting of a single layer of rounded cells with suberized walls (*fig. 6*). Inside this is a narrow zone of vascular tissue, whose elements run circularly; then a wide zone, consisting of small bundles running vertically, and so closely packed together that it is generally impossible to distinguish their limits. Bounding the two vascular rings on the inside is a band of sclerified cells which are in contact with the pith. As the photograph shows, leaf-trace bundles make their way into the central cylinder through wide gaps in this four-layered ring, and it may be clearly seen, even in unstained sections, that along the edges of such a gap the external suberized endodermis is continuous with the inner sclerified layer. All of the large leaf-trace bundles pass through such gaps, but the roots leave the central cylinder without causing a gap, as has been observed in plants of various groups. In the pith of the central cylinder are scattered many

bundles, nearly all of which are amphivasal, and where the nodes are crowded, as they are at the very base of the stem, the amphivasal condition is retained by bundles from one node to another, though in the more elongated internodes, found a little higher in the stem, only collateral bundles occur. The contrast between the upper and the basal nodes is indeed striking, for the former show no amphivasal bundles running longitudinally in the pith, except the enlarged leaf-traces. This feature of the aerial node may be partly accounted for by the thinness of the diaphragm in which run the anastomosing bundles, which are generally amphivasal.

AMPHIVASAL BUNDLES

Although these have been repeatedly reported as occurring in the subterranean stems of monocotyledons (see STRASBURGER, 4, p. 348, footnote; DEBARY, 2; SCHULZE, 5)³, the only references to their occurrence in grasses that have been found are by STRASBURGER (4) and JEFFREY (9). DUVAL-JOUVE (1) figures the rhizomes of many grasses, but shows no amphivasal bundles. Yet an examination of the nodes of some of the same species shows that the bundles in question occur here. Two sorts must be distinguished in this family: (1) the swollen portion of a leaf-trace bundle, the xylem consisting largely of a mass of tracheids running irregularly; (2) the type usually figured, the xylem forming simply a ring of vessels. The features of the first class have been described under *Avena*. Such a bundle is always enclosed by an endodermis which generally has pitted or reticulated walls, and shows, in addition to the ordinary metaxylem elements, a large number of reticulated tracheids, which almost or quite enclose the phloem. All the species examined show these bundles, from hydrophytes such as *Zizania* to xerophytes such as *Ammophila*, and there appears to be no relation between the size which a bundle attains at its widest part and the condition under which the species grows. If, as already suggested, these bundles serve to store up water, it might be expected that they would be poorly developed in aquatics, but the only peculiarity of the bundles found in such plants is the slight lignification of the xylem, a char-

³ Since the above was written, HOLM has reported the occurrence of amphivasal bundles in the rhizome and also the aerial stem of *Croomia pauciflora* (Amer. Jour. Sci. 20:50-54. 1905).

acter shared by all the bundles of such plants. Quite commonly, the bundles are surrounded by a layer of parenchyma rich in chlorophyll. This suggests that the node is an active assimilating organ. Bundles of the second class—amphivasal bundles as usually understood—are found in the nodes of the great majority of the grasses examined, but are especially numerous in the following species: *Coix lachryma*, *Paspalum stoloniferum*, *Panicum sanguinale*, *Sorghum halepense*, *Leersia oryzoides*, *Phalaris arundinacea*, *Calamagrostis canadensis*, *Avena barbata*, *Panicularia americana*, *Panicularia nervata*, *Festuca arundinacea*, *Triticum sativum*. The fact that they are practically confined to the nodal regions, suggests that they are associated with bundle fusions, and this assumption has been amply borne out by observation. Further, since the bundles which fuse are usually traces of leaves which come off higher up, it appears that the occurrence of such bundles is to be referred to the leaves. The closed mode of venation, prevalent in the monocotyledons, involves that a large number of bundles shall run down parallel to one another through the petiole or sheathing base of the leaf. In the grasses the numerous bundles are accommodated in the leaf-sheath, which frequently encircles the stem for somewhat more than 360°. The large number of bundles cannot at once find room in the vascular ring, which we may believe constitutes the primitive stele in both dicotyledons and monocotyledons, according to the results of JEFFREY (8), and CHRYSLER (10). Hence the leaf-trace bundles, or some of them, pass into the inside of the central cylinder, and sooner or later join other bundles. It will be readily seen that a bundle lying in the pith has a better chance to orient itself with regard to some other bundle which it may join, than has a bundle which merely fits itself into a gap in a vascular ring (e. g., the leaf-trace of a fern such as *Adiantum*). Hence it is not surprising to find that before two bundles of a monocotyledon fuse, they swing around, so that phloem fuses with phloem, and the xylem accordingly surrounds the compound bundle. How far beyond the point of fusion of the bundles this amphivasal condition persists, is a feature which varies greatly. In most of the grasses the collateral structure is soon resumed, but the example of *Zizania* shows that, at the base of the stem where the nodes are crowded, the amphivasal condition

may continue through several internodes. This probably accounts for the prevalence of these bundles in the rhizomes of monocotyledons, where they were first observed. A comparison of the aerial and subterranean nodes of the grasses under study has not yielded results of great significance; most species show no noticeable difference in the number of amphivasal strands in the two cases. But in *Andropogon furcatus*, *A. scoparius*, *Chrysopogon avenaceus*, *Zizania aquatica*, and *Phleum pratense*, the amphivasal strands are distinctly more numerous in the basal nodes. No examples of the opposite condition have been found. QUEVA found in *Gloriosa* (7) that the amphivasal bundles are connected with the origin of a branch. Among the grasses, *Phalaris arundinacea*, *Paspalum stoloniferum*, *Sporobolus Wrightii*, *Coix lachryma*, and *Zea Mays* show these bundles at the point of origin of branches, but in other species only collateral bundles could be discovered at these places. Too much importance should not be attached to the few cases named, in view of the fact that the sedges uniformly show amphivasal bundles associated with leaves and not with branches, as PLOWMAN has shown (10). This is one reason for considering the grasses a more specialized group than the sedges; in fact it may be premised that the amphivasal condition originally connected with leaf-traces has in the Gramineae spread to the branches. The occurrence of amphivasal bundles in the leafy reproductive axis of *Zea*, while they are rare in the main stem, deserves emphasis. While many of the grasses show amphivasal bundles in all the nodes, in this highly developed genus the bundles in question have nearly disappeared from the ordinary nodes, but have persisted in the conservative region named. STRASBURGER proposes (4, p. 348) a physiological explanation for the occurrence of these bundles, viz., that the amphivasal structure is favorable for the taking up of reserve materials stored in a rhizome, but this explanation is not in accord with the accepted view that elaborated food is carried not by the xylem, but by the phloem. Examination of serial sections leads to the opinion that the mechanical necessities of bundle fusion rather than considerations of absorption of food have been the determining factor in producing these bundles.

If we accept the view advanced above, that these bundles are to

be associated with the large number of leaf-trace bundles of the monocotyledons, their phylogenetic significance is considerable. The ferns and dicotyledons have a comparatively small number of leaf-trace bundles; amphivasal bundles are absent in the former and rare in the latter group, but are widely distributed in the monocotyledons, which accordingly appear to represent a more recent and highly specialized group. In the most highly organized members of the Gramineae, such as *Zea*, is shown a tendency to reduce the number of amphivasal strands, but even in such cases they may linger on in the reproductive axis. JEFFREY (9) has called attention to the fact that in highly organized families, such as Iridaceae and Orchidaceae, these bundles disappear even from the reproductive axis.

CAMBium.

A feature of the vascular bundles of *Avena barbata*, not so far mentioned, is represented, in *fig. 9*, which shows a bundle from the stem at a distance of about 1^{mm} above one of the upper nodes. That the tissues are immature is shown by the presence of protoplasm and a nucleus in certain of the vessels. The shrunk protophloem is represented by the dark band at the outer edge of the bundle, and the metaphloem as usual has its elements arranged irregularly. Between these elements and the vessels are a number of rows of flattened cells, radially arranged, corresponding well to the cambium of dicotyledons. This feature is not confined to the young stem, as is seen in *fig. 10*, which represents a bundle from above one of the lower nodes of the same plant. A few tangential divisions are to be seen in the leaf-trace bundle shown in *fig. 1*, though cambial activity here is slight. Toward the node and farther up in the internode and sheath, this peculiarity is not shown by the bundles, but at the regions mentioned most of the bundles have a more or less clear indication of cambium.

In the leaf-sheath of *Andropogon argenteum* (*fig. 11*), at a distance of 1-2^{mm} above its insertion on the stem the larger bundles show an unmistakable cambial layer. From the small amount of phloem or xylem showing radial arrangement of its elements, it appears that the cambium is functional for only a short time. Sections through the leaf-sheath, cut 5^{mm} above the one shown in the figure, still exhibit a layer of radially arranged cells exterior to the xylem,

but the cells have thicker walls and a rounded outline, indicating that in that region the period of activity of the cells is past. The stem of this plant does not show good examples of cambium, nor do *A. scoparius* or *A. furcatus* show the feature, even in the leaf-sheath.

A further example is shown in *fig. 12*, which represents a bundle from the stem of *Erianthus Ravennae* 1-2^{mm} above the level of insertion of the leaf-sheath. A similar appearance is presented by the bundles of the sheath. The leaf-trace bundles of *Zizania* frequently show a large amount of their phloem radially arranged, in spite of the fact that dicotyledonous aquatics generally show a marked reduction of their cambium. The examples so far cited include only the more striking instances of cambium found in the family. More or less plain evidences of cambium have also been observed in the following species: (1) In both stem and leaf-sheath; *Coix lachryma*, *Panicum crus-galli*, *Avena sterilis*, *Lolium italicum*, *L. perenne*. (2) In stem; *Tripsacum dactyloides*, *Miscanthus sinensis*, *Pennisetum longistylum*, *Panicum sanguinale*, *Leersia oryzoides*, *Sporobolus Wrightii*, *Calamagrostis canadensis*, *Arundo Donax*, *Avena sativa*, *Briza maxima*, *Panicularia americana*, *Bromus inermis*, *Triticum sativum*. The occurrence of a cambium in the region just above the nodes in grasses recalls the well-known power which members of this family possess of bending upward at these regions if the stem is by any means laid horizontally. In this connection it is of interest to note that PLOWMAN (11) has found only traces of cambium in the sedges, and in line with this, the stems of sedges are unable to right themselves if bent over into a horizontal position. Miss ANDERSSON (3) has reported the occurrence of a more or less plain cambial zone in the young plants of representatives of many monocotyledonous families. She calls attention to the similarity between the bundles in the seedling of *Lilium* and those in *Ranunculus*. The only grass referred to is *Zea*, in which the mature bundles often show a radial arrangement of the cells between xylem and phloem, as is illustrated by the well-known figure in SACHS' *Text-book*. From the occurrence of cambium in the tuberous stems of *Gloriosa*, QUEVA (7) has already concluded that the monocotyledons are derived from dicotyledons. In the case of the grasses it would seem that the cambium possessed by the ancestors

has been retained in the regions where it is of use. On the other hand, it may be argued that we have here the first appearance of a feature which in the dicotyledons becomes prevalent. But why should the cambium appear only at the nodes, where it is of use? It may be regarded as almost axiomatic that the need for a structure is not a sufficient cause for its appearance. So it seems more reasonable to read the evidence in the way first suggested, viz., that we have here a relic of a structure which was present in the ancestors of the grasses, but has disappeared from most parts of the plant and from most families of monocotyledons, and is retained above the nodes of grasses in connection with their power of bending at these regions. Thus the evidence favors the derivation of the grasses from ancestors having a cambium.

The stele of the grass stem has evidently departed widely from the primitive protostele or siphonostele. It has been repeatedly shown that reproductive axes are able to retain ancestral characters. An examination of this region in seventeen species of grasses belonging to seven of the tribes has failed to disclose any instances where the stele presents the primitive type described by PLOWMAN (II). This result seems to confirm the opinion derived from other considerations, that the Gramineae represent a more specialized group than the Cyperaceae. These considerations may now be stated categorically:

(1) The grass family has adapted itself to every habitat, from salt marsh to pampas, and shows every gradation in habit from the bamboo downward. The sedges are prevaillingly hydrophytes, and few of them attain a considerable size.

(2) The hollow stem characteristic of most grasses has probably been derived from a solid stem such as is present in the sedges and most monocotyledonous families.

(3) Amphivasal bundles are not found in so large a proportion of species nor are they as numerous in an individual in the grasses as in the sedges.

(4) In practically all of the grasses the leaf-trace bundles are of at least two ranks, while the sedges show no such distinction.

(5) The floral axis of the grasses does not present the simple type of stele shown by some sedges.

On the other hand, the open sheath of the grass leaf may be considered to be more primitive than the closed sheath of the sedges. Further, the cambium found in the grasses is here considered to be a primitive feature. But on the whole the Gramineae are to be regarded as a more highly specialized family than the Cyperaceae, though the families are evidently very closely related.

Certain anatomical features of the grasses, such as the distribution of the amphivasal bundles, seem to have an important bearing on the phylogenetic position of the family among monocotyledons, but since the anatomy of the group is as yet very imperfectly known, a discussion of this point would be premature.

SUMMARY AND CONCLUSIONS.

1. The grasses depart considerably from the scheme proposed by VON MOHL for the course of the bundles, chiefly owing to the stem being hollow in most cases. The leaf-trace bundles are of at least two ranks; of these the largest penetrate most deeply as they enter the central cylinder, generally receiving one or more bundles on each flank as they pass downward to the lower part of the node; the smaller leaf-trace bundles do not penetrate deeply into the central cylinder, but after anastomosing with other bundles pass downward either in the cortex or at the inner border of this. At the next node lower, these cortical bundles anastomose with one another, and then with the bundles of the central cylinder which have come from fusions with leaf-trace bundles at the next node above.

2. The leaf-trace bundles, especially the larger ones, undergo a marked change as they enter the stem. This consists in the appearance of a distinct endodermis, and in an increase in the xylem, leading to the formation of a greatly swollen amphivasal bundle. Below the node these bundles resume the collateral type.

3. Amphivasal bundles of the ordinary type, though absent in the aerial internodes, are very commonly found in the nodes, and arise by fusion of collateral bundles which are generally leaf-trace bundles. In some species they are more numerous in the nodes at the base of the plant, and where such nodes are crowded, the bundles may retain the amphivasal condition through successive internodes. The presence of amphivasal bundles in reproductive branches of plants in which these bundles are scarce in ordinary

nodes, points to their being an ancestral feature, which, in highly organized members, has disappeared from most parts of the plant, but is retained in the conservative flowering axis. It appears that the amphivasal bundles so characteristic of monocotyledons, in all probability made their appearance in connection with the entry of numerous leaf-trace bundles into the nodes, but that secondarily, in certain instances, they are found to be related to branching.

4. A well-marked, though generally short-lived, cambium occurs in the bundles just above the node or near the base of the leaf-sheath in certain grasses. This fact is considered to lend support to the view that monocotyledons have been derived from some group possessing a cambium, probably the dicotyledons.

5. The anatomical features of the grasses point to their being a more highly specialized family than the sedges.

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LITERATURE CITED.

NOTE.—Practically nothing bearing immediately on the subject of this research has been found in the older literature, so it is not cited here. References to it may be found in DEBARY (2), and the text of KNY's *Wandtafeln*.

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EXPLANATION OF PLATES I AND II.

PLATE I.

FIG. 1. *Avena barbata*; leaf-trace bundle in the leaf-sheath 1^{mm} above its insertion on the stem. $\times 130$.

FIG. 2. Same; swollen and amphivasal condition of a leaf-trace bundle in the middle region of node. $\times 130$.

FIG. 3. *Phalaris arundinacea*; section through upper part of a node; near the outside are the leaf-trace bundles, alternating large and small; just internal to these are the nests of amphivasal bundles. $\times 30$.

FIG. 4. Same; one of the nests of amphivasal bundles more magnified; on three sides are leaf-trace bundles. $\times 150$.

FIG. 5. *Zea Mays*; one of the large amphivasal bundles from a node of a reproductive branch. $\times 115$.

FIG. 6. *Zizania aquatica*; part of stele and cortex in basal region of the stem. Two gaps with their leaf-trace bundles are visible. $\times 35$.

PLATE II.

FIG. 7. *Panicularia americana*; section 1^{mm} above node, showing two cortical bundles. $\times 45$.

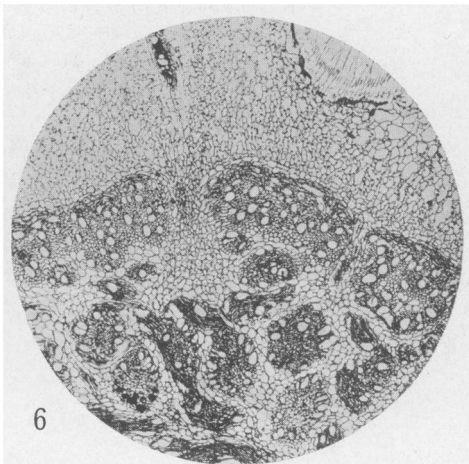
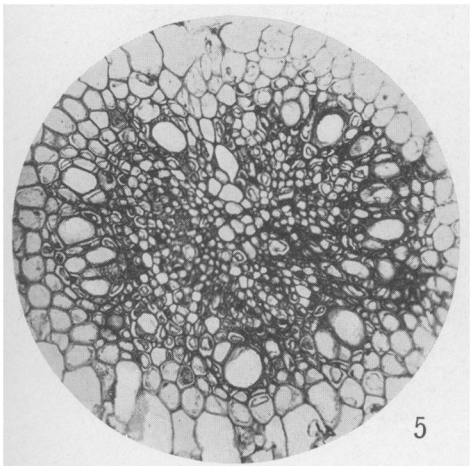
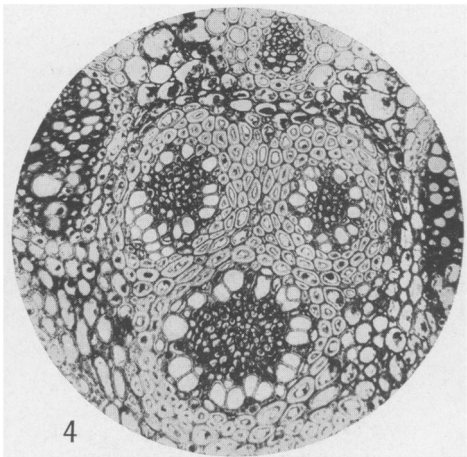
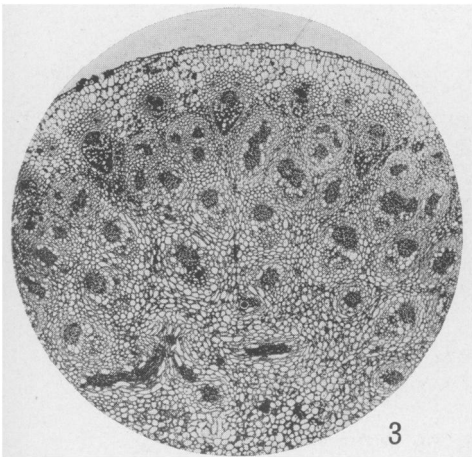
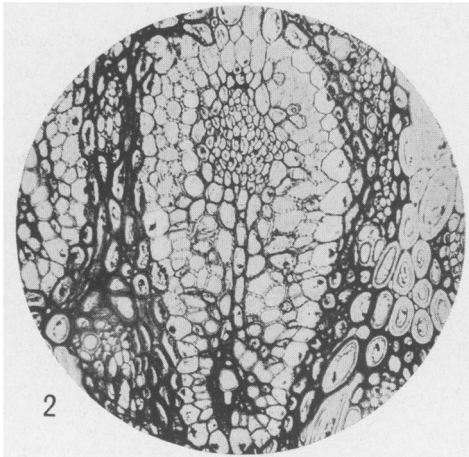
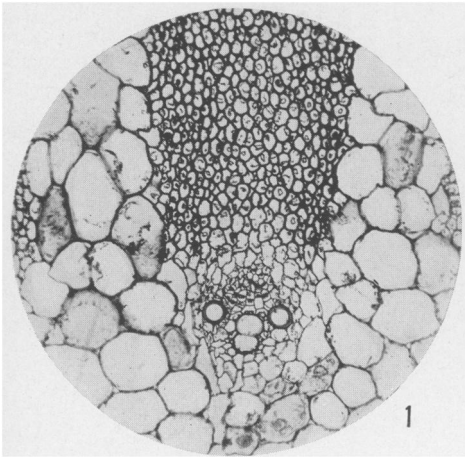
FIG. 8. Same; section from upper part of the node, just above insertion of leaf-sheath. The cortical bundles are connected by a ring-shaped anastomosis. $\times 45$.

FIG. 9. *Avena barbata*; bundle from a young stem 1^{mm} above insertion of the leaf-sheath, showing cambium. $\times 150$.

FIG. 10. Same; bundle from the same position in a mature stem. $\times 150$.

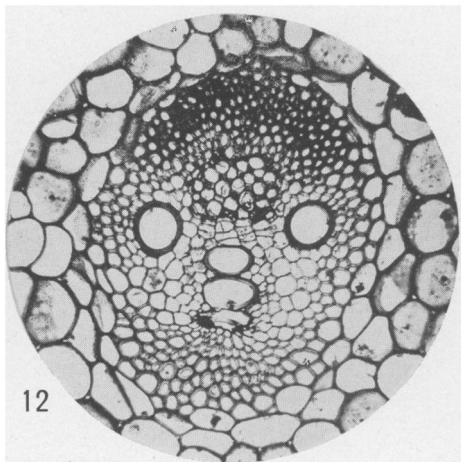
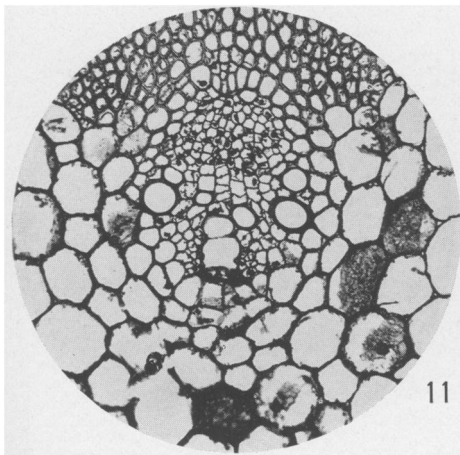
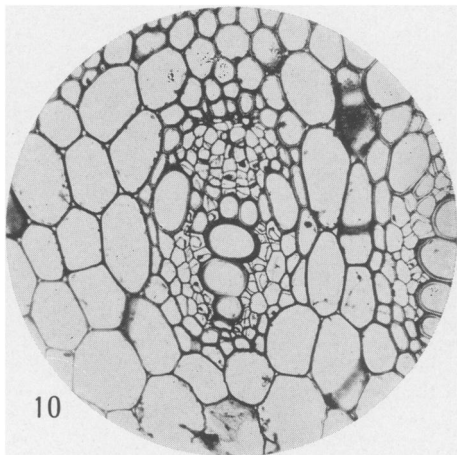
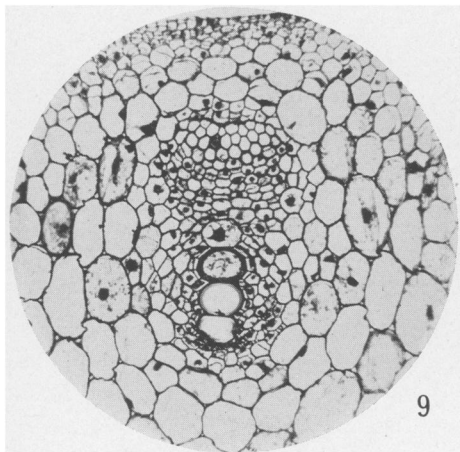
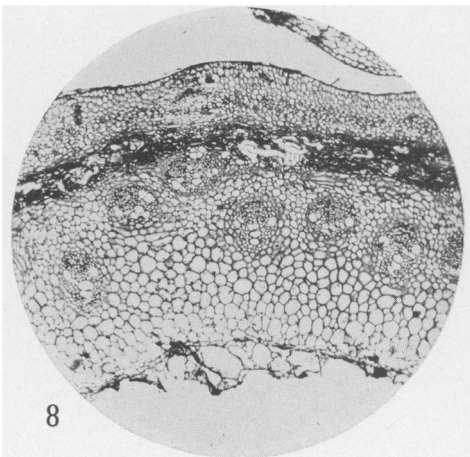
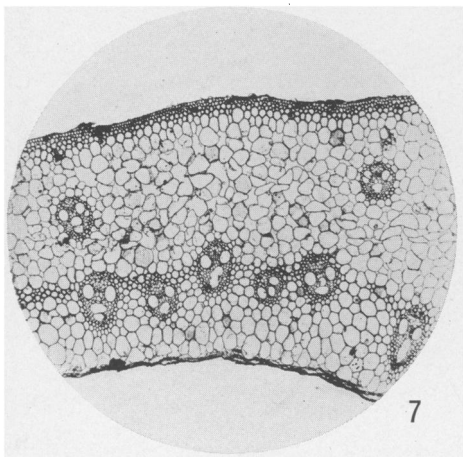
FIG. 11. *Andropogon argenteum*; bundle from the leaf-sheath 1-2^{mm} above its insertion on the stem, showing cambium. $\times 150$.

FIG. 12. *Erianthus Ravennae*; bundle from the stem a short distance above a node. $\times 150$.



M. A. C. photo.

CHRYSLER on NODES OF GRASSES



M. A. C. photo.

CHRYSLER on NODES OF GRASSES